

XXXV.—On the Development of the Chelonians.

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I HAVE for nine years been engaged in collecting materials for a history of the development of the Chelonians, and I think of soon publishing the result of my researches. I have had an opportunity of examining the embryo in a considerable number of fresh eggs of *Emys europæa*, from its first appearance to the period when the toes of the feet would soon have appeared. For the knowledge of the succeeding periods of development, I had at my disposal two almost mature embryos of *Chelonia* and *Testudo* and ten very young Chelonians of different species (*Chelonia Mydas*, *Sphargis coriacea*, *Trionyx gangeticus*, *Tr. ocellatus*, *Emys europæa*, *Em. mauritanica*, *Cinosternum scorpioides*, *Cin. pensylvanicum*, *Platemys Spixii*, *Pentonyx . . .*).

The development of the embryos remains some time quite in accordance with the general type of the development of the most perfect vertebrated animal. It is especially the respective position of the ventral and dorsal laminae and of the spinal marrow which does not differ in the least, either at the commencement or at a later period, from what we observe in the higher vertebrated animals. The remark of M. de Baër, "that, in the young embryos of *Emys europæa*, the ventral laminae are attached to the dorsal laminae, at the point where the latter are united above to close the dorsal furrow, and that the back itself is thus somewhat depressed," is a very pardonable error, as the embryo is attached very strongly to the yolk, which is very tenacious in that species. Nor can the assumption of my scientific friend be proved, "that, in the Chelonians, the extremities are not detached from the upper (or external) surface of the ventral and dorsal laminae, as in the other vertebrated animals, but from their lower (or internal) surface." I have found, on the contrary, in the youngest embryos of *Emys europæa*, the extremities situated externally, in the same parts of the body, and in the same manner as in the embryos of the mammals, birds and Saurians.

The embryos of *Emys europæa*, the extremities of which are so developed that the digits must soon have appeared, but the ribs of which were not yet visible, resemble excessively the very young embryos of the Saurians and mammals. Their body in particular is neither flattened above or below, nor too wide for its length, and its dorsal part is insensibly continued (without interruption, without elongated margin, as in the adult Chelonians) with the neck, with the lateral parts and with the tail. Starting from the examination of these young embryos and from the observations

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made in other Chelonians which were not entirely developed, I shall endeavour to give a sketch of the manner in which the development of the Chelonians takes place in general.

After a somewhat advanced development of the extremities in the embryos, the dorsal and ventral surfaces of the body are gradually flattened, more or less, according to the different species, and two lateral apophyses begin to shoot from all the twelve or thirteen vertebræ of the trunk. Most of these apophyses, being developed like the eight intermediate pairs of ribs, acquire in a short time a very considerable length. As they are in general but slightly curved, their extremities are turned more outwards than downwards. Thus, by the very rapid and considerable elongation of these ribs, the sides of the body, containing their extremities turned outward, are pushed much forward on each side, and the trunk becomes very wide between the anterior and posterior feet, situated at its commencement and termination.

It is a fact as singular as characteristic of the Chelonians, that their last two ribs, remarkable for their longitudinal growth, that is to say, in general the eighth and ninth pairs, are turned directly backward, whereas the second pair (but not in all the Chelonians) have a somewhat anterior direction. The chorion then forms a fold on each side, at the spot where the extremities of the very prolonged ribs (second or eighth pair) are situated. This fold stretching out, projects anteriorly beyond the anterior foot to reach the neck, and posteriorly beyond the hindermost foot to reach the tail; lastly, it meets, on the neck and on the root of the tail, the similar fold of the opposite side, and the two unite to form a single circular fold, which then separates the back of the sides of the body. In some Chelonians, especially the marine, this fold expands slightly during the development; in others, principally in the *Trionyx*, it becomes extremely broad, especially the part situated above the tail. Much later, that is to say after the hatching of the embryos, the ribs, before remarkable for their length, but up to that time, all or nearly all of a cylindrical form, become also much wider. This increase in width begins from the spot where the neck unites with the body, and advances thence more or less toward the extremities; it becomes so considerable, that the bodies on all the ribs, from the complete absence of intercostal muscles, are on each side in contact and adhere, either perfectly, that is to say in their whole length, as in the genera *Emys*, *Terapene*, *Testudo*, *Trionyx*, or almost perfectly, that is to say for the greater part of their length, as in the *Chelonia*. The intercostal nerves and some vessels situated at first between the ribs, then pass beneath them. In return, the first and the last rib become much shorter than the others, and always continue very narrow and thin. Their relations also

with the neighbouring ribs differ much from those of the intermediate ribs; for, as the latter increase greatly in width, the second exceeds the first, and the last but one surpasses the last so much that it covers it more or less entirely. Soon after the eight pairs of intermediate ribs have begun to widen, a branch protrudes superiorly from each rib, near the vertebral column. This branch continually increasing passes beyond the rare and thin dorsal muscles; the two sacro-spinal muscles (situated on the summit of the ribs, throughout the length of the body) unite with the spinal apophysis of the vertebræ of the same rib, and become quite as wide as the body itself of the rib. The spinal apophyses make their appearance, even before the hatching upon the second vertebra up to the eighth. They remain very short; but, contrary to the general laws of development of vertebrated animals, they increase so much in width, after their ossification, that they form at last a series of horizontal plates of the average size.

I cannot adopt the opinion which supposes these plates to be formed in the subcutaneous cellular tissue, independently of the vertebral column, in the chorion itself or below it; that they unite afterwards with the vertebræ, and that the remarkable width of the eight pairs of intermediate ribs is also the result of contact, and subsequently of an adhesion with the osseous plates formed above these ribs. On the contrary, these assumptions are refuted by my observations.

After the successive expansion of the bodies of the eight pairs of intermediate ribs, of their superior branch, exclusively peculiar to the Chelonians and of the spiny apophyses of the same vertebræ, an osseous plate is finally formed by the contact and adhesion of the corresponding margins of all these parts, composed of numerous pieces, which extends to form the carapace above and covers the viscera. To increase and complete this shell, already very considerable, we observe other osseous plates unite with it. They are formed on the back, wholly independent of the vertebral column and of the ribs, in a very thick and solid layer of the subcutaneous cellular tissue, and must be considered as the external skeleton (cutaneous skeleton) of the animals*. Their number varies in the different species of Chelonians. In the genus *Trionyx* only one disc is found; it is situated on the neck immediately in front of the dorsal vertebræ. There are also some discs in the posterior margin of the carapace in some species of *Trionyx*; but they remain cartilaginous. Besides this nuchal plate, which is always very large, several small subcutaneous plates are also developed in most of the Chelonians. Among these, a small number only originate above the last

* These terms are borrowed from the nomenclature of M. Carus.

dorsal and the sacral vertebræ, all the rest are developed in the posterior and lateral parts of the circular cutaneous fold (limbus), the anterior portion of which is in great part filled by the anterior half of the nuchal disc, which enters progressively into that portion of the circular fold.

After the flattening of the ventral ribs, there is also, between the teguments and the muscles, in the layer of a thick and solid cellular tissue which joins these different parts, a development of some cartilaginous pieces, of which the plastron is subsequently formed. I have not been able to determine the moment at which their formation commences. The inconsiderable development of the plastron in the oldest embryos, and in the individuals scarcely hatched, leads me to conjecture that it is hardly formed before the middle of the embryonic life, and at all events relatively later than the sternum of birds and mammals. The cartilaginous pieces themselves, appearing as the foundation of the plastron, are at first, for the most part, simple bands, very narrow and thin, forming two pairs, situated one before and the other behind the umbilical aperture. Between these two pairs a very considerable space still exists at the period of hatching. Moreover, there is generally formed, or at least in most of the Chelonians (excepting the *Sphargis* ?), between the anterior extremities of the two even front pieces, a small odd or fifth cartilaginous plate. Subsequently other numerous osseous pieces are developed in these different cartilages, commonly or perhaps always nine in number. Their respective size is very variable, according to the different species of Chelonians; for, either they grow so much one before another that they meet at their corresponding margins, throughout their length, so as to form a perfectly united plastron, or their growth continues more limited, and then they form a plastron open in the centre, or merely a narrow ring, as is probably the case with the *Sphargis*. Moreover, the development of the plastron differs also in the fact, that its circumference, and especially its length, become relatively greater in some species of Chelonians than in others. It then passes beyond the neck and the tail below forming an elongation clothed by the chorion alone, whilst this elongation is wanting in other species. This difference probably depends on the previous existence or not on the ventral side of the body, below and before the anterior feet, and below and behind the posterior feet, of a transversal fold of the chorion, into which the growing plastron might enter. Thus it is probable that the species which exhibit the elongation just described are those in which such a fold already existed. This fact is rendered very probable by the examination of the Chelonians of the genus *Trionyx*, in which this fold is in fact found; but it is

scarcely filled by the parts of the plastron, little developed in this genus.

A specific and very remarkable feature in the Chelonians is subsequently the relation of their bones of the trunk with the very solid subcutaneous cellular tissue, forming a layer of little thickness and commonly considered cartilaginous. All the osseous pieces contiguous to this layer, namely, the spiny apophyses of the vertebræ from the second up to the eighth, the eight pairs of intermediate ribs, the supplementary plates of the shell, and often also all the pieces of the plastron, after having lost by re-absorption on their external surface the periosteum, come in contact with the subcutaneous cellular tissue. This happens after the hatching of the embryo and principally on the ribs, so that the periosteum disappears gradually, from the upper extremity (nearer to the vertebræ) toward the lower extremity. In the marine Chelonians it does not disappear wholly on the lower extremity, but only as far as the part of the ribs which never expand to any extent. As soon as the osseous substance of this part comes in immediate contact with the subcutaneous cellular tissue, numerous medullary cellules appear in the direction of this tissue, which, at least in the commencement, are externally open. By degrees their number increases considerably, and the bones which I have just named become at the same time stronger and very porous, although there may be, according to the species, a marked difference in their porosity. The cellules are not principally filled with fat, as is the case in more perfect vertebrated animals, and even in the Chelonians, in the bones further removed from the chorion; they are filled by the subcutaneous cellular tissue. This tissue enters gradually by the apertures of the cellules as by a radiation of numerous small roots, and collects there always in proportion to their growth. Nevertheless the layer of this tissue situated between the bones and the chorion constantly diminishes, not only relatively, but also in part absolutely, so that it seems wholly to be wanting on the carapace and the plastron in some Chelonians, especially in the *Emys europæa*.

If we consider, as usual, the plastron of the Chelonians as a portion of the nervous skeleton and as the homologue of the sternum of the other vertebrated animals, we must also admit that the bones composing the scapular and the pelvic arches are situated in a wholly contrary manner to the general disposition of these parts (when they exist) in the other vertebrated animals. They would be situated so as to remain wholly inexplicable, according to our present knowledge of the development of the animals. But, from some facts, I believe I can prove evidently that the plastron is nothing else than a part of the cutaneous skeleton, and that, in

an anatomical point of view, it has nothing in common with the sternum of other animals. This supposition once admitted, we may refer the situation of the bones of the shoulder and the basin of adult Chelonians to the relations existing in other animals. There is then no longer anything extraordinary in the arrangement of these parts, but only something specific produced by the curious development of the dorsal parts of the body. With respect to the position of the scapulæ, they are situated before the ribs in older embryos and in young Chelonians, and it is more than probable that they occupied this position even before the development of the ribs had made any sensible progress, and that they were not merely protruded by the ribs in consequence of the rapid growth of the body in width. In fact, the first pair of ribs, near and a little in advance of which they are situated in older embryos and young individuals, is scarcely remarkable either for its very great length or its width; it is on the contrary extremely short and thin, so that a displacement of the scapulæ becomes impossible. Moreover, we see in some fishes, some Saurians (*Titigna sincoides*), and even in a mammal (*Ornithorhynchus*), the scapulæ occupying a similar position in front of the ribs. In the *Didelphis virginiana*, the whole scapula, or at least the lower part with the scapular articulation, is situated anterior to the ribs, and it thus becomes probable that in these animals also, at least in a period previous to their development, the entire scapula, before it acquires its oblique position and its considerable width, is situated in front of the ribs. In other mammals the scapulæ (although they are never so protruded as in the Chelonians and the *Ornithorhynchi*) meet in the first period of their development much further in advance than in the subsequent periods. In the hog, for instance, the scapula, a little after the formation of the anterior foot, covers the two anterior ribs of the corresponding side. When it is not perceptible as a separate part, it does not at the commencement go beyond the first rib, whilst it extends from the first up to the seventh in adult hogs.

Lastly, the direction of the scapulæ in the Chelonians does not differ much from that which is observed in the *Ornithorhynchi* and several Saurians, in which they also occur perpendicular. Their situation below the osseous parts of the back in the adult Chelonians is produced subsequently by the successive development, for even in the oldest embryos they are in immediate contact, by their upper extremities, with the layer of the subcutaneous cellular tissue.

The metamorphosis which I have just described results from the considerable expansion of the second pair of ribs, extending

beyond the adjoining parts of the skeleton, the first pair of ribs and the scapulæ, in the form of a dome.

The position and articulation of the pelvis of the Chelonians differ absolutely in nothing from the normal type which vertebrated animals present as regard the relations of position of the pelvian bones; for the coxal bones of the Chelonians are joined to the os sacrum as in the mammals and in the Saurians in general. Thus they offer nothing in particular, except that they are covered by other osseous parts. This covering, which we find over the whole pelvis of the Chelonians, results in a small part from an enlargement of the penultimate pair of the ribs, but principally from the development of the cutaneous skeleton, for almost the whole posterior part of the shield, forming in most of the Chelonians a roof above and behind the pelvis, is composed of osseous pieces, developed near the chorion and independent of the vertebral column and the ribs.

With respect to the fact that we find both the humeri and the femora of the Chelonians covered above, and in some species also more or less underneath, this is generally in consequence of the longer or shorter lateral folds of the chorion, in which peculiar osseous pieces belonging to the cutaneous skeleton are developed. It is likewise owing to this, that of the eight pairs of intermediate ribs very much elongated and directed outwards, the last two are moreover turned greatly backwards, and in several Chelonians, but not in all, the two anterior ones forwards; the former extend beyond the coxal articulation, the latter beyond the scapular articulation.

These facts appear to me to demonstrate the error of the common assertion, that in the Chelonians the bones composing the shoulder and the pelvis are within the body. The arrangement of the peritoneum in the Chelonians proves it even in a positive manner, for it does not envelope on the two sides any of the osseous parts of the shoulder nor of the pelvis with their muscles: it clothes them only on a single side, that turned towards the intestines. Behind, it enters, as in the mammals, at a distance in the cavity of the upper pelvis, clothes in part its internal surface and the muscles which are fixed there, and passes thence over the viscera placed in this pelvis. Finally, it proceeds beneath the dorsal part of the body up to the scapulæ (situated, as I have said, far anteriorly), enveloping the lower surface of the kidneys, the internal genital parts, the inferior surface, and the external margin of the lungs, with almost their whole upper surface adhering to the ribs, and the portion of the ribs extending laterally beyond the lungs and the urinary organs. After having passed the lungs, which reach in front the scapulæ, over the

